

OBSERVATIONS ON THE SYSTEMATICS, GEOGRAPHIC AND
STRATIGRAPHIC DISTRIBUTION AND ORIGIN OF *DIPLOMOCERAS*
CYLINDRACEUM (DEFRANCE, 1816) (CEPHALOPODA: AMMONOIDEA)

by

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(With 17 figures)

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ABSTRACT

The heteromorph ammonite genus *Diplomoceras* has a near world-wide distribution in the Maastrichtian, but records as far back as early Campanian have been quoted. Due to the generally fragmentary nature of the material and intraspecific variation, systematics of the genus are disputed. According to recent comprehensive reviews by Kennedy (1986a, 1987 *et seq.*), the genus appears to be monospecific, consisting of the type species, *Diplomoceras cylindraceum* (Defrance, 1816) only. Differential preservation of internal moulds of the phragmocone and body chamber respectively, and similarities in suture lines suggest that the origins of *Diplomoceras cylindraceum* may be sought in *Neoglyptoxoceras annulatum* (Collignon, 1969), a species thus far known only from the lower Campanian of Madagascar.

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Figure 1

Diplomoceras cylindraceum (Defrance, 1816). SAM-PCZ9551 from locality 113, KwaZulu, St Lucia Formation. Maastrichtian a or b. An internal mould that retains the ribbing. $\times 1$.

INTRODUCTION

The heteromorph ammonite *Diplomoceras cylindraceum* (Defrance, 1816), type species of the genus *Diplomoceras* Hyatt, 1900, is a conspicuous faunal element of the Maastrichtian stage by virtue of its near-cosmopolitan distribution, paper clip-like coiling and, in some instances, gigantic size. It is also amongst the last surviving ammonites before the demise of the Order Ammonoidea at the end of the Cretaceous Period.

Diplomoceras typically consists of several straight shafts, connected by a series of variable U-shaped sections (Figs 1–6). Because of this loose coiling, post-mortem fragmentation is universal and complete specimens of the species are unknown. The early whorls were thought to have been coiled in a helix (cf. Wright 1957: L227; Matsumoto 1959: 165; Klinger 1976: 81), but this misconception was probably based on a helically coiled heteromorph from Seymour Island, Antarctic Peninsula, described and figured as *Anisoceras* (*Diplomoceras*) *notabile* Whiteaves, 1903 by Kilian & Reboul (1906: 15 (*pars*), pl. 5, pl. 6 (fig. 1) only). These specimens are definitely not conspecific with *D. notabile*, and may possibly be *Nostoceras* (*Bostrychoceras*) *sanctaeluciense* Klinger, 1976, but without having seen the actual specimens we can not be sure. Juvenile specimens tentatively referred to *D. notabile* by Matsumoto (1984: 312, pl. 8 (fig. 3)) and Matsumoto & Miyauchi (1984: 68, pl. 27 (fig. 2); text-fig. 11A) suggest that the paper clip-like coiling already occurs from a very early ontogenetic stage. Gigantic specimens with estimated total uncoiled lengths of c. 2.5 metres have been recorded from Seymour Island as *Diplomoceras maximum* Olivero & Zinsmeister (1989: 629, figs 2.5, 4.1–4.4, 5.1–5.4), exceeding in size by far the largest late Cretaceous (straight) baculitids (see Klinger & Kennedy 2001). Up to now, no complete specimen has been found, and the adult aperture is unknown.

The whorl section is generally circular, or slightly compressed or depressed (Fig. 2E). Ornament on the shell consists of simple, uniform ribs with no tubercles (Figs 5–6). Constrictions, if present (cf. Henderson *et al.* 1992, fig. 5A–B; Kennedy 1999: 653, fig. 12.1–2) are rare. On internal moulds, however, ornament differs between the phragmocone and body chamber. Internal moulds of the phragmocone are usually (Figs 2B, 3–4), but not always (Figs 1, 2A, C–D) smooth whereas internal moulds of the body chamber retain the ribbing. This conspicuous anomaly has been noted on several occasions (see Olivero & Zinsmeister 1989: 627; Henderson *et al.* 1992: 141; Kennedy 1999: 657), and according to Olivero & Zinsmeister (1989), can be ascribed to the thickening of the nacreous shell layer below the ribs on the phragmocone, and may be considered diagnostic of the genus *Diplomoceras*. Apart from shell structure, the latter authors also provided details of muscle scars, previously recorded by Jones (1961), and speculated on the mode of life and buoyancy control of *Diplomoceras*. The suture line (Fig. 7A–C) is deeply incised with a large bifid lateral (*L*) and umbilical (*U*) lobe, and a small, trifid internal (*I*) lobe. The saddles all have very narrow stems.

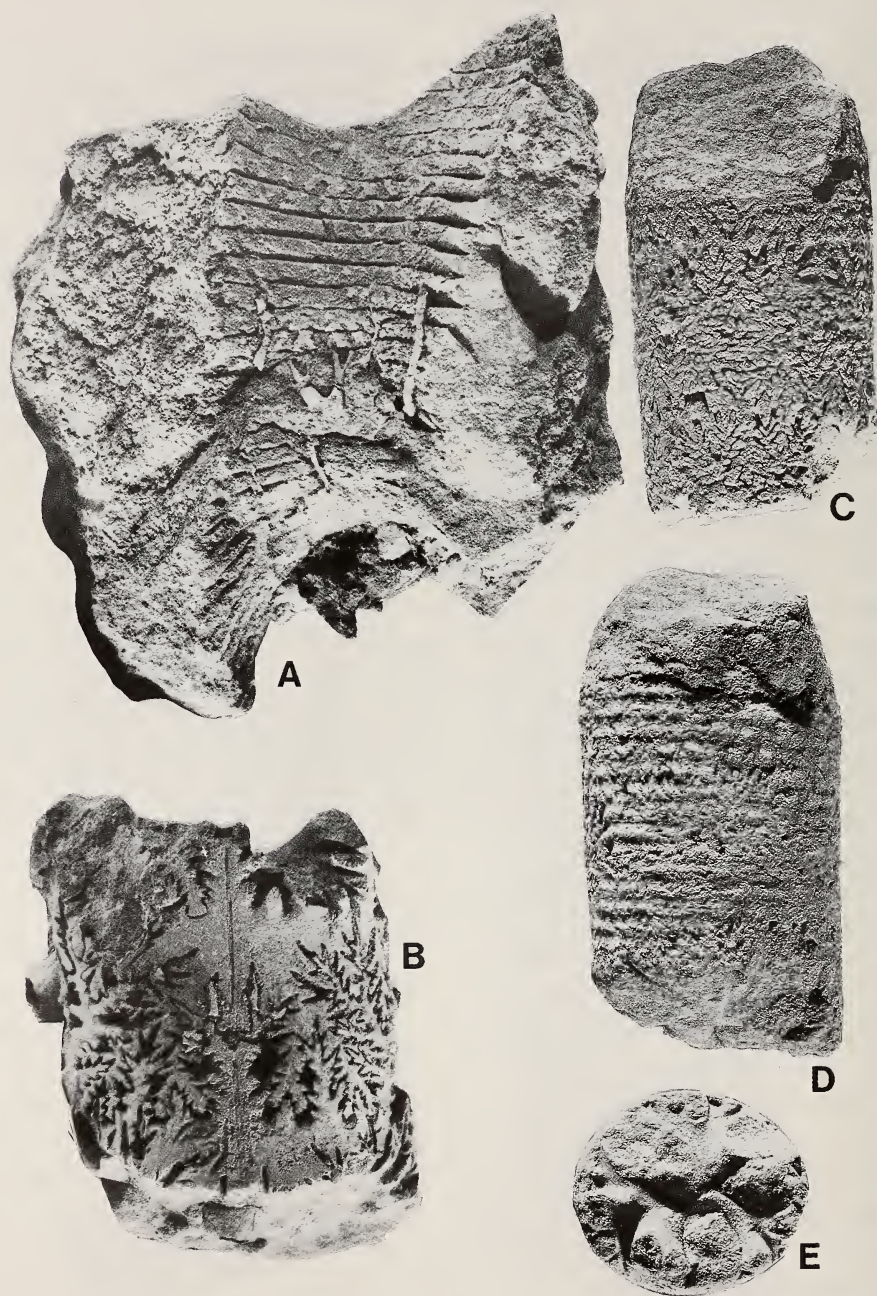


Figure 2

Diplomoceras cylindraceum (Defrance, 1816). A. SAM-PCZ7940 from locality 20, KwaZulu, St Lucia Formation. Maastrichtian a or b. B. SAM-PCZ7904 from the same locality as A. C-E. SAM-PCZ17356 (ex H105/9) from locality 116, KwaZulu, St Lucia Formation, Maastrichtian a. All $\times 1$.

SYSTEMATICS

The geographic and stratigraphic distribution of the genus *Diplomoceras* is largely dependant on whose taxonomic procedure is followed. Conservatively, the following species have been referred to the genus with differing degrees of confidence:

1. *D. cylindraceum* (Defrance, 1816)—the type species.
2. *D. notabile* Whiteaves, 1903.
3. *D. lambi* Spath, 1953.
4. *D. maximum* Olivero & Zinsmeister, 1989.
5. *D. australe* Hünicken, 1965.

Apart from these, several species from California have been attributed to the genus by Anderson (1902, 1958), but these are either uninterpretable from the figures and descriptions, or are synonyms of the above.

Kennedy (1987), in his revision of the ammonite fauna of the type Maastrichtian, and subsequently (Kennedy & Henderson 1992; Henderson *et al.* 1992), based on Indian and Western Australian material respectively, regard *D. notabile*, *D. lambi* and *D. maximum* as junior synonyms of *D. cylindraceum* because of overlapping dimensions of the whorl section and density of ribbing.

Based on the compressed whorl section ($Wb:Wh = 1,26$ and $1,24$) of the holotype, the only other species that may be referable to the genus according to these authors is *D. australe*. However, according to Macellari (1986: 9), the specimens referred to this species by Hünicken appear to be deformed, and may be referred to *D. lambi*, that is, *D. cylindraceum* as interpreted by Kennedy (1987, and subsequent discussions).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

If the taxonomic procedure of Kennedy (1986a, 1987 *et. seq.*) is accepted, the genus *Diplomoceras* is monospecific, comprising the type species, *D. cylindraceum* (Defrance, 1816) only.

Diplomoceras cylindraceum has a near world-wide distribution (Figs 8–9), being most common in high northern and southern latitudes, but is remarkably rare in equatorial regions and is apparently absent from the Middle East (Zeev Lewy pers. comm.) and Angola and Nigeria. It ranges throughout the whole of the Maastrichtian stage.

There are, however, earlier, Campanian records of *D. cylindraceum*, some apparently extending back to the early Campanian (Alabushev & Wiedmann 1997). Upper Campanian records from Japan include those of Matsumoto & Morozumi (1980), Matsumoto (1984) and Matsumoto & Miyauchi (1984). In Zululand (Klinger & Kennedy, this volume 110(6), p. 303) *D. cylindraceum* occurs mainly in the Maastrichtian, but a single specimen is known from the uppermost Campanian of Kennedy & Klinger's (1975) locality 111 (Klinger & Kennedy, this volume 110(6), p. 303). In Antarctica, the species has been dated as late Campanian–early Maastrichtian and late Maastrichtian as *D. lambi* and *D. maximum* respectively. In northern Spain, Gallemi *et al.* (1983) have records of *D. notabile* from the upper Campanian. Machalski (1996) also tentatively records



Figure 3

Diplomoceras cylindraceum (Defrance, 1816). A. IRSNB 10292 ex Ubaghs Collection from the upper Maastrichtian Calcaire de Kunraed of Kunrade, Limburg, The Netherlands. B. IRSNB 10262 (IG 8261 ex De Jaer Coll.) from the same horizon and locality as A.

D. cylindraceum from the upper Campanian of the Piotrawin section in Central Poland. Kűchler & Odin (2001) also record *D. cylindraceum* from the upper Campanian of Tercis, France.

The stratigraphic distribution of the species in southern Sakhalin reported by Alabushev & Wiedmann (1997) is difficult to interpret. According to these authors, *D. cylindraceum* s.s. is restricted to the upper Maastrichtian and is the index fossil for the eponymous zone as proposed by them for northeast Russia. *Diplomoceras notabile*, on the other hand, is reported (Alabushev & Wiedmann 1997: 15) to occur in the lower Campanian of Sakhalin and the lowermost Campanian of northwestern Kamchatka but, according to their Table 1 (p. 29) occurs throughout the whole of the Campanian. The specimen figured as being from the lower Campanian (Alabushev & Wiedmann 1997, pl. 4 (fig. 1)) is part of a juvenile shell, and is generically indeterminable; it could be referred to either *Diplomoceras* or *Glyptoxoceras*.

Even if the record of the first occurrence of *D. cylindraceum* in the lower Campanian is incorrect, its definite occurrence from the upper Campanian to the end of the Maastrichtian makes it one of the longest ranging heteromorph ammonite species of the Cretaceous Period.

ORIGIN OF *DIPLOMOCERAS CYLINDRACEUM*

Despite its near-cosmopolitan occurrence and long stratigraphic range, the origins of the species and genus have received little attention. Matsumoto & Miyauchi (1984: 68) suggested an origin in *Scalarites* (together with *Glyptoxoceras*), but no further details were given.

Based on similarities in suture lines, mode of coiling, ornamentation in general, and differences in ornament on internal moulds of the phragmocone and body chamber respectively, we suggest an origin for *Diplomoceras cylindraceum* in the poorly known and apparently endemic material from Madagascar referred to the two genera, *Neoglyptoxoceras* Collignon, 1969 and *Epiglyptoxoceras* Collignon, 1969. *Neoglyptoxoceras*, type species *Neoglyptoxoceras magnificum* Collignon, 1969 (1969:30, pl. 523 (fig. 2065), p. 35, pl. 526 (figs 2074–2075)) (Fig. 10A–B) and *Epiglyptoxoceras*, type species *Epiglyptoxoceras abnorme* Collignon, 1969 (1969: 35, pl. 526 (fig. 2076)) are both relatively common in the lower Campanian of Madagascar. Apart from the type species, *Neoglyptoxoceras* is further represented by *N. perangustum* Collignon, 1969 (1969: 38, pl. 527 (fig. 2078)) (Fig. 11) and *Epiglyptoxoceras* by *E. annulatum* Collignon, 1969 (1969: 41, pl. 529 (fig. 2083)) (Figs 12–15) and *E. giganteum* Collignon, 1969 (1969: 40, pl. 528 (figs 2081–2082)) (Fig. 16) in the lower Campanian. *Neoglyptoxoceras* persists to the middle Campanian of Madagascar as *Neoglyptoxoceras serti* Collignon, 1970 (1970: 15, pl. 613 (figs 2286–2289)) (*non* Müller & Wollema, 1906). As their names indicate, *Neoglyptoxoceras* and *Epiglyptoxoceras* are superficially similar to the genus *Glyptoxoceras* Spath, 1925 in being ornamented by ribs only, but differ from that genus in their much larger size.

According to Collignon, the two genera differ from each other in the number of saddles and lobes in their suture lines. *Neoglyptoxoceras* was reported to have four saddles instead of three, and three lobes instead of two as in *Epiglyptoxoceras*.



Figure 4

Diplomoceras cylindraceum (Defrance, 1816). IRSNB 10257 (IG 6521 ex Ubaghs Collection) from the upper Maastrichtian Calcaire de Kunraed of Kunrade, Limburg, The Netherlands. $\times 1$.

Unfortunately, Collignon's sutural terminology is confusing and needs to be clarified. According to the sutural terminology of Wedekind (1916), reviewed by Kullmann & Wiedmann (1970), the adult suture of Cretaceous heteromorph ammonites consists of four lobes, *E* (External), *L* (Lateral), *U* (Umbilical) and *I* (Internal); the three saddles are referred to by their positions relative to the lobes, i.e. *E/L*, *L/U*, *U/I*.

The following is Collignon's original diagnosis of *Neoglyptoxoceras* (1969: 35) with our interpretation of the sutural terminology in parenthesis.

"...et surtout par sa cloison qui compte 4 selles au lieu de 3, et 3 lobes au lieu de 2. Ces 4 selles sont de forme caréé, avec lobule médian plus ou moins oblique. Le premier lobe (*L*) très étalé, très volumineux, deux fois plus long que le siphonale (*E*); le deuxième (a large median incision of the saddle *U/L*) est réduit, en forme d'étoile; le troisième (*U*) presque aussi fort et long que le premier, présente une branche externe prépondérante. Lobule antisiphonal (*I*) très allongé".

The "extra" lateral lobe in *Neoglyptoxoceras* is in fact no more than a large, median incision of the saddle *L/U*, which is very broad. In *Epiglyptoxoceras*, this saddle (*L/U*) is constricted at the base, and the median incision is reduced (compare Collignon 1969, figs 2074–2076, 2081–2083). This suture pattern differs in no significant respects from that of *D. cylindraceum* (See Fig. 7). We agree with Wright (1997: L250) in regarding *Epiglyptoxoceras* as a synonym of *Neoglyptoxoceras*, albeit for different reasons; Wright considered *Epiglyptoxoceras* to be based on a pathological specimen. We do not think that the sutural differences between the type species of the two taxa merit separation at generic level, and as first revising authors select the name *Neoglyptoxoceras* for the taxon.

Apart from similar sutures, *Neoglyptoxoceras* resembles *Diplomoceras* in being ornamented by ribs only. A further, and in our consideration, crucial similarity is in the difference in ornament between internal moulds of the phragmocone and body chamber in both *Diplomoceras* and *Neoglyptoxoceras*. It is well known that internal moulds of *D. cylindraceum* are generally smooth, whereas the same mode of preservation of the body chamber produces distinct ribbed ornament. This anomaly has been ascribed to abnormal thickening of the middle nacreous layer below the ribbing on the phragmocone, and is considered characteristic of the genus *Diplomoceras* by Olivero & Zinsmeister (1989: 627, with additional references). A similar, though not identical situation exists in *Neoglyptoxoceras*. Here, ribbing occurs on both phragmocone and body chamber, but the strength and shape of ribbing changes dramatically on internal moulds at the end of the phragmocone and beginning of the body chamber. This can be clearly seen on the holotype and paratype of *N. magnificum* (Collignon 1969, pl. 523 (fig. 2065); pl. 526 (figs 2074–2075)) (Fig. 10A–B); see also Fig. 17). Similar differences in ribbing on the body chamber and phragmocone on internal moulds have also been recorded in *Glyptoxoceras rugatum* by Henderson *et al.* (1992) and may possibly be a diagnostic feature of some of the genera referred to the subfamily Diplomoceratinae Spath, 1926.

The ribbing of *Neoglyptoxoceras magnificum* is too coarse, and the suture line a little too different for it to be considered directly ancestral to *D. cylindraceum*. The fine ribbing of *Neoglyptoxoceras annulatum* (Collignon, 1969) (Collignon 1969: 41, pl. 529 (figs 2083–2084)) (see also Figs 12–15), however, is perfectly compatible with that of



Figure 5

Diplomoceras cylindraceum (Defrance, 1816). IRSNB 10290, ex Ubaghs Collection from the upper Maastrichtian Calcaire de Kunraed of Kunrade, Limburg, The Netherlands. The specimen retains silicified shell. $\times 1$.

D. cylindraceum. In addition, the coiling in *N. annulatum* changes from crioconic in the early stages of growth (Fig. 15) to more elliptical, tending towards straightening of the shaft in the adult stage (Figs 12–14). In fact, some specimens of *N. annulatum* (Figs 13–14) and *D. cylindraceum* (Kennedy 1987, pl. 23 (fig. 1)) (Fig. 3A) have near-identical coiling. In addition, in larger specimens of *N. annulatum* the whorl section changes from slightly compressed at the smaller adapical end to near-circular at the larger abapertural end.

A curious feature of *N. annulatum* is that successive sutures, rather than interdigitating as in *D. cylindraceum*, are clearly separated, producing smooth zones on the internal mould (Figs 12A–B, 13–14). As yet, we have no explanation for this distinctive feature, but similar, widely-spaced sutures also occur in *Glyptoxoceras* cf. *subcompressum* (Forbes 1846) (Kennedy 1987: 179, pl. 26 (figs 1–6, 8–9, 13–14, 19–21)) from the upper Maastrichtian of Kunrade, The Netherlands.

We believe that all the necessary elements for the “Bauplan” of *D. cylindraceum* may be found in *N. annulatum*. Apart from the smooth band between successive sutures, these elements include similar suture lines, the change in ornament on internal moulds from the phragmocone to the body chamber, the adult whorl section, and progressive tendency towards elliptical coiling on the outer whorl, eventually leading towards the straight limbs of *D. cylindraceum*. With the exception of a single possible specimen from KwaZulu (Fig. 10C) the genus *Neoglyptoxoceras* appears to be endemic to Madagascar. Previous records of *Neoglyptoxoceras* from Europe, e.g. (*Neoglyptoxoceras* (?) *retrorsum* in Kennedy 1986b: 106, pl. 16 (figs 1–4, 6–7); pl. 17 (figs 1–2); text-fig. 38) are best referred to *Glyptoxoceras*.



Figure 6

Diplomoceras cylindraceum (Defrance, 1816). IRSNB 10290, ex Ubaghs Collection from the upper Maastrichtian Calcaire de Kuraed of Kunrade, Limburg, The Netherlands. The specimen retains silicified shell. $\times 1$.

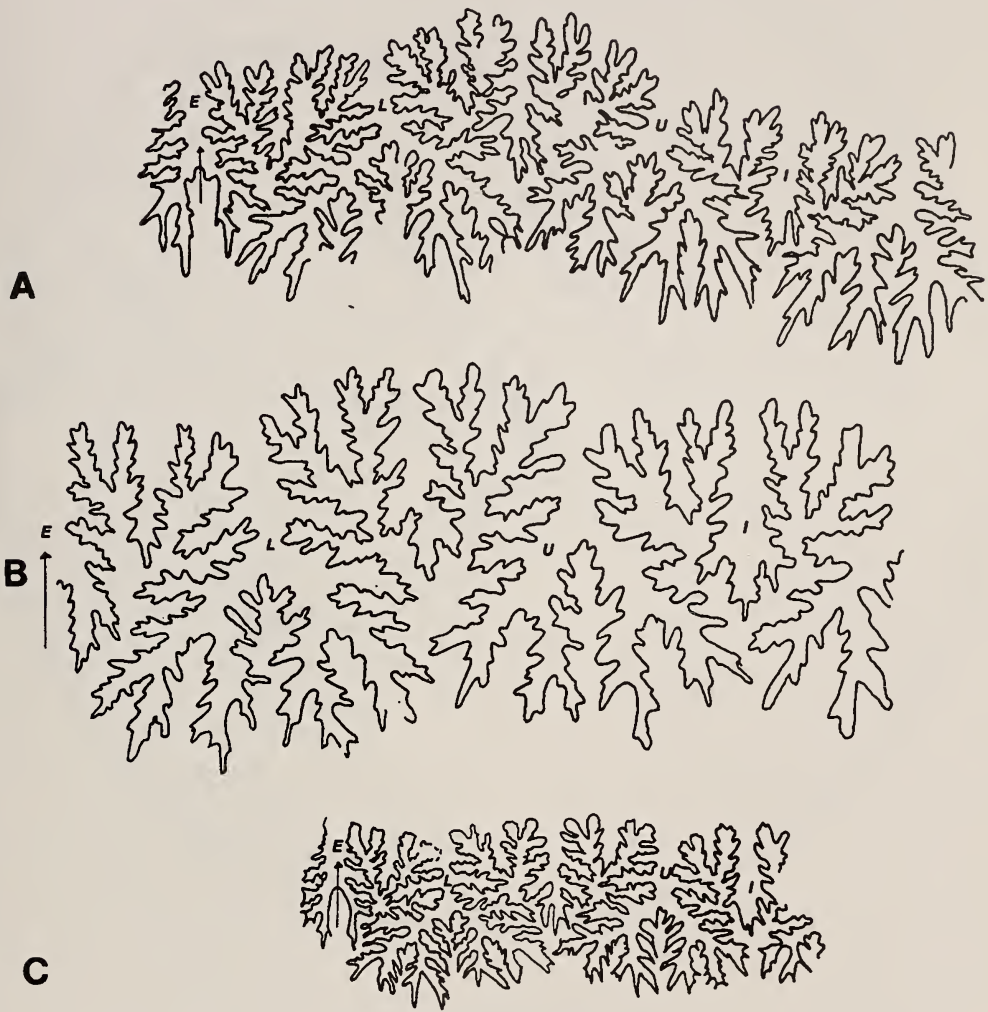


Figure 7

Suture line of *Diplomoceras cylindraceum* (Defrance, 1816). A. Copy after Kennedy 1986a, text-fig. 7M. B. Copy after Macellari 1986, fig. 15. C. Copy after Jones 1963, fig. 15.



Figure 8 above (and see Figure 9)

Geographic distribution of *Diplomoceras cylindraceum* (Defrance, 1816). France, Biscay Region (Ward & Kennedy 1993), Pyrénées Atlantiques (Kennedy 1986c), Tercis (Küchler & Odin 2001); Cotentin Peninsula (Kennedy 1986a); Northern Spain (Wiedmann 1962); Italy (Mariani, 1898); The Netherlands (Kennedy 1987); Belgium, the Mons Basin (Kennedy 1993); northern Germany (Schlüter 1872); Denmark (Birkelund 1993); Poland (Błaszkievicz 1980; Machalski 1996); Austria (Kennedy & Summesberger 1986); The Ukraine (Kennedy & Summesberger 1987); Bulgaria (Tzankov 1982); Serbia (ex Yugoslavia) (Petkovic 1953); Don Basin, Russia (Naidin 1974); Caucasus & Crimea (Naidin & Shimanskij 1959); European Russia (Mikhailov 1951); Arctic Siberia (Dundo 1971);

Continued next page



Figure 9

Continued from previous page:

Northwestern Kamchatka & southern Sakhalin (Alabushev & Wiedmann 1997); Tunisia (Robaszynski *et al.* 2000); South Africa (KwaZulu) (Klinger 1976); Madagascar Collignon 1971); South India (Kennedy & Henderson 1992); Pakistan, Baluchistan (Kennedy 1999 *in* Fatmi & Kennedy); Western Australia (Henderson *et al.* 1992); Antarctic Peninsula (Olivero & Zinsmeister 1989); Argentina (Hünicken 1965); Chile (Stinnesbeck 1986); Brazil (Maury 1930); California (Anderson 1902, 1958); British Columbia (Whiteaves 1903); Alaska (Jones 1963); Japan, Hokkaido (Matsumoto 1984); and possibly West Greenland (Birkelund 1965) and New Zealand (Henderson 1970). This list is not intended to be complete, and references are mainly restricted to one per locality.

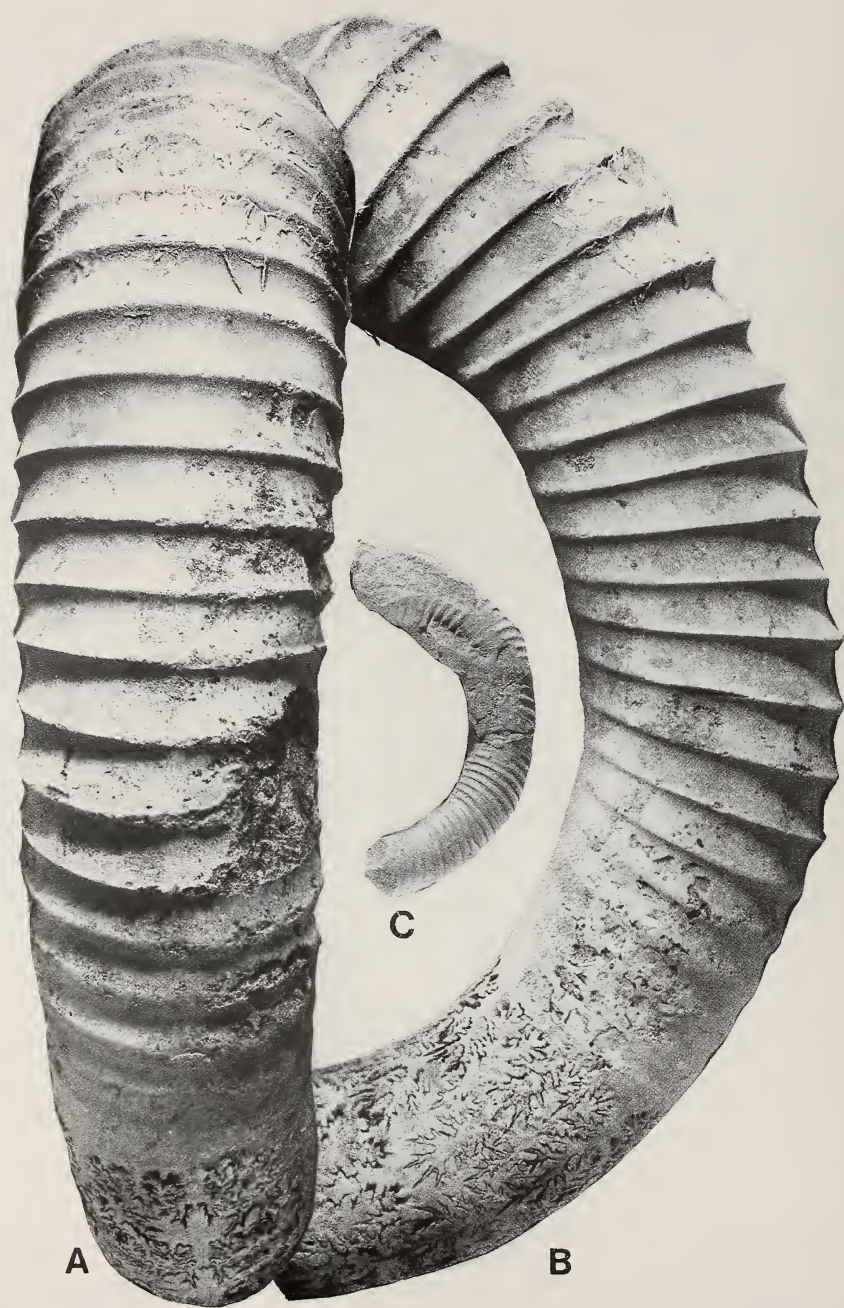


Figure 10

A–B. *Neoglyptoxoceras magnificum* Collignon, 1969. The holotype, GD12074 from Gisement 162 de la Coupe de Berere I (Belo sur Tsiribihina), lower Campanian, Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi*, subzone of *Hourcquiella bererensis*, level of *Neogauthiericeras zafimahovai*. C. *Neoglyptoxoceras* sp. cf. *N. sarta* Collignon 1969 non Müller & Wolleemann, 1906 from locality 109C, KwaZulu, St Lucia Formation, Campanian III.



Figure 11

Neoglyptoxoceras perangustum Collignon, 1969. The holotype, GD12078 from Gisement 162, lower Campanian Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi* subzone of *Hourcquiella bererensis*, Coupe de Berere I (Belo sur Tsiribihina). $\times 1$.



Figure 12

Neoglyptoxoceras annulatum (Collignon, 1969). A–B. GD12083, the holotype, from Gisement 312 du Km 16,200 de la Coupe Ampolypoly–Antsirasa–Behamotra (Belo sur Tsiribihina), lower Campanian, Zone of *Menabites boulei* & *Anapachydiscus arrialoorensis*. Note the smooth zone between successive sutures. C. Early whorls of *N. annulatum*, GD14013 from Gisement 162 de la Coupe de Berere I (Belo sur Tsiribihina), Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi*, subzone of *Hourcquiella bererensis*. Level of *Neogauthiericeras zafimahovai*.



Figure 13

Neoglyptoxoceras annulatum (Collignon, 1969). GD14014 from Gisement 312 du Km. 16,200 de la Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), lower Campanian, Zone of *Menabites boulei* & *Anapachydiscus arrialoorensis*. In the figure, the lower part of the shaft has been cropped to fit the page size. $\times 1$.



Figure 14

Neoglyptoxoceras annulatum (Collignon, 1969). The same specimen as figured in Fig. 10. In the figure, the lower part of the shaft has been cropped to fit the page size. $\times 1$.



Figure 15

Neoglyptoxoceras annulatum (Collignon, 1969). GD14015 located imprecisely as Berere, lower Campanian. Early, criocone whorls. $\times 1$.

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Figure 16

Neoglyptoxoceras giganteum (Collignon, 1969). GD12081, the holotype from Gisement 307 du Km. 15,500 de la coupe Ampolypoly–Antsirasa–Behamotra (Belo sur Tsiribihina), lower Campanian, Zone of *Menabites boulei* & *Anapachydiscus arrialoorensis*, subzone of *Rabeiella orthogonia*.

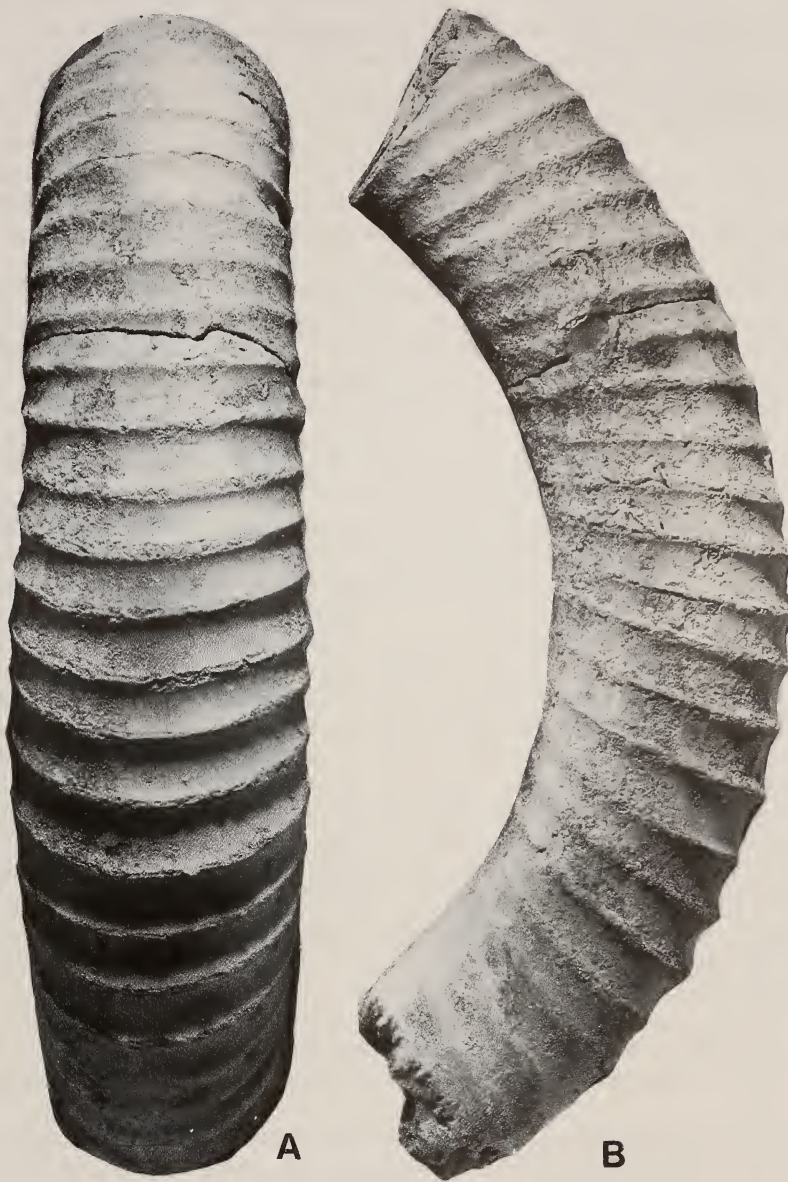


Figure 17

Neoglyptoxoceras magnificum Collignon, 1969. GD12075, part of the paratype figured by Collignon (1969: 35, pl. 526 (fig. 2075)) from Gisement 161, de Coupe de Berere I (Belo), Zone of *Anapachydiscus wittekindi* & *Eulophoceras jacobi*, subzone of *Hourcquiella bererensis*, level of *Neogauthiericeras zafimahovai*.

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